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Lowest drought sensitivity and decreasing growth synchrony towards the dry distribution margin of European beech

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Abstract

Aim: Climate limits the potential distribution ranges of species. Establishment and growth of individuals at range margins is assumed to be more limited by extreme events such as drought or frost events than in the centre of their range. We explore whether the growth of beech is more sensitive to drought towards the dry distribution margin and more sensitive to frost towards the cold distribution margin. Furthermore, we aim to gain insight into the adaptive potential of beech towards both the dry and cold distribution margins.

Location: European gradient from the dry (Spain) to the cold (Poland, Sweden) distribution margin of beech.

Taxon: European beech (*Fagus sylvatica* L.).

Methods: We applied a range-wide dendroecological study to analyse spatial and temporal trends in climate–growth relationships. We further investigated negative growth anomalies and growth synchrony towards the range margins.

Results: We found beech to be drought sensitive across its whole range, except at the dry distribution margin. Furthermore, sensitivity to winter temperature was not found in the centre or at the cold distribution margin, but at the southern distribution margin. Growth synchrony was lower at the dry than at the cold distribution margin.

Main conclusions: Beech seems to be adapted to drought at the dry distribution margin with a high adaptive potential indicated by the lowest growth synchrony along the gradient. At the cold distribution margin, cold events in winter and spring were less important for growth than drought. Still, the importance of spring frost for beech growth appears to increase in recent decades. Considering a projected north-eastward shift of the distribution range, beech is likely facing drought stress in combination with spring frost risk at the cold margin which could lead to a hampered range expansion.

KEYWORDS

climate sensitivity, cold edge, cold events, dendrochronology, dry edge, *Fagus sylvatica*, forest ecology

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1 | INTRODUCTION

The potential distribution ranges of species are limited by climate and they are projected to shift to higher latitudes and to higher elevations in times of global warming (Lenoir, Gégout, Marquet, Ruffray, & Brisse, 2008; Parmesan, 2006; Parmesan et al., 1999; Sykes, Prentice, & Cramer, 1996). Ecological theory suggests that the climate sensitivity of tree growth increases towards marginal populations (Fritts, 1966). Many studies highlight wide-spread tree growth limitations by drought (e.g. Babst et al., 2019; Breshears et al., 2005). Moreover, drought can determine the distribution limit of tree species towards the equatorial edge (Normand et al., 2009; Pigott & Pigott, 1993; Sykes et al., 1996). Thus, increasing temperature and drought might lead to range contractions at the dry equatorial edge. Towards the poleward edge, the native ranges of many woody species may also be determined by minimum temperatures in winter (Kreyling, Schmid, Aas, & Higgins, 2015; Sakai & Weiser, 1973), or, as suggested by other authors, by freezing temperatures in spring during and after bud burst (Kollas, Körner, Randin, & Vetaas, 2014; Körner et al., 2016; Lenz, Hoch, Vitasse, & Körner, 2013; Muffler et al., 2016). Summing up, growth responds to environmental stressors such as drought and can be used as indicator for vitality (Dobbertin, 2005). Hence, growth decline is often associated with range limits.

Due to the strong link between climate and species distribution ranges, the current climate change may be one of the factors forcing genetic adaptation within populations (Jump & Peñuelas, 2005). Generally, local adaptation is expected to be of particular importance at distribution limits, where the selective pressure of environmental conditions is assumed to be stronger than in its range centres, and where genetic mixing is limited due to geographic isolation (Choler, Erschbamer, Tribsch, Gielly, & Taberlet, 2004; Kawecki, 2008; Paul, Sheth, & Angert, 2011).

Across Central Europe, European beech (*Fagus sylvatica* L.) is the dominant forest tree and is found across wide environmental and climatic gradients (Bolte, Czajkowski, & Kompa, 2007; Fang & Lechowicz, 2006; Leuschner, Meier, & Hertel, 2006). Growth of beech is also highly sensitive to drought (Di Filippo et al., 2007; Jump, Hunt, & Peñuelas, 2006; Lebourgeois, Bréda, Ulrich, & Granier, 2005; Scharnweber et al., 2011; Zimmermann, Hauck, Dulamsuren, & Leuschner, 2015), which can lead to growth decline and thus might limit its southern distribution range (Piovesan, Biondi, Di Filippo, Alessandrini, & Maugeri, 2008; Saltré, Duputié, Gaucherel, & Chuine, 2015; Seynave, Gégout, Hervé, & Dhôte, 2008; van der Maaten et al., 2017). However, there is evidence that beech can recover quickly from drought stress, and that drought-exposed marginal populations might be more resistant to severe drought events than originally thought (Dittmar, Zech, & Elling, 2003; Hacket-Pain & Friend, 2017; van der Werf, Sass-Klaassen, & Mohren, 2007). Cavin and Jump (2016) even found that drought resistance increases from the core to the dry margin of the distribution range, probably due to local adaptation (Thiel et al., 2014). Moreover, populations at the equatorial edge that persisted as relict populations during

past climatic changes might again persist as isolated populations in the future, with a smaller population decline than in the continuous range (Vilà-Cabrera, Premoli, & Jump, 2019). Here the ecological and not geographical marginality plays an important role in explaining the higher decline in the centre. As the likelihood of drought events is projected to increase with climate change (IPCC, 2013), a better understanding of the spatial pattern of the response of beech to drought across its distribution range is needed.

Towards the northern and northeastern distribution margin, the distribution range of European beech is not just determined by drought events, but also by winter frost and extreme spring frost events (Bolte et al., 2007). However, the influence of cold events on the growth of beech is controversial. According to Lenz, Hoch, and Vitasse (2016), the high frost resistance of dormant beech buds and cambial meristems contradicts the absolute minimum temperature in winter as a predictor for the northern cold distribution margin. Furthermore, while spring frost events can lead to a strong reduction in radial growth of beech, growth recovers in the years after the event (Dittmar, Fricke, & Elling, 2006; Dittmar et al., 2003; Príncipe et al., 2017). In contrast, at the northeastern margin of the distribution range, beech growth was found to be sensitive to severe winter frost (Augustaitis et al., 2016), though studies on frost sensitivity of beech at its cold distribution margin are still rare (Weigel et al., 2018). An increased cold sensitivity and growth decline at the northern margin might be due to a reduced nutrient uptake induced by fine-root die-off during extreme cold events and reduced root activity in cold soils (Reinmann, Susser, Demaria, & Templer, 2019; Sanders-DeMott, Sorensen, Reinmann, & Templer, 2018; Schenker, Lenz, Körner, & Hoch, 2014). Moreover, Malyshev, Henry, Bolte, Arfin Khan, and Kreyling (2018) found no differences in winter dormancy and budburst forcing requirements in a common garden experiment among beech populations along a gradient from the centre towards the northeastern distribution margin, hinting at the absence of local adaptation towards the cold distribution margin. These findings are supported by the low genetic variation among populations in the centre and towards the leading edge of the species' distribution, while diversity is high at the equatorial edge (Magri et al., 2006). Consequently, in consideration of a projected shift of the distribution range beyond the current cold distribution margin (Kramer et al., 2010; Saltré et al., 2015), it is important to better understand the response to winter and spring cold events of beech. This is particularly important as the magnitude of cold events may persist, and their frequency may even increase in future (Kodra, Steinhäuser, & Ganguly, 2011; Petoukhov & Semenov, 2010), leading to an increased risk of frost damage due to earlier onset of growth in times of climate change (Augsburger, 2013; Liu et al., 2018; Vitasse, Schneider, Rixen, Christen, & Rebetez, 2018).

Under harsh climatic conditions at the distribution margins, strong environmental drivers (drought, frost events) would commonly affect a whole population and lead to high growth synchrony within the population (Andreu et al., 2007; Macias, Andreu, Bosch, Camarero, & Gutiérrez, 2006; Shestakova et al., 2016). According to



this logic, low growth synchrony may indicate a higher within-population diversity in response to the given stressor, which would be a potential basis for natural selection favouring well-performing individuals. Hence, low synchrony could indicate conditions under which selection could lead to rapid local adaptation in the face of changing environmental conditions, whereas high synchrony would imply lower adaptive potential even in the presence of strong stress. However, studies on growth synchrony of beech at the cold as well as at the dry distribution margin are missing. Such studies could give valuable insights into the adaptive potential of beech and could provide a better understanding of the adaption to cold and drought events at the distribution margins.

Here we analysed climate sensitivity and growth synchrony of beech along a European gradient contrasting the centre of the distribution range with the dry and the cold distribution margins. Growth sensitivity to climate was assessed by analysing climate–growth relationships, such that stronger correlations represent higher sensitivity to any particular climatic parameter. We hypothesized that (Ia) drought sensitivity of growth is more pronounced in the centre than at the southern distribution margin due to well-developed local adaptation of dry-marginal populations, and (Ib) cold sensitivity increases towards the northeastern distribution margin due to a presumed absence of local adaption. Based on the first hypothesis, we furthermore expected that (IIa) growth synchrony is lower at the southern, dry distribution margin compared to the centre due to a lower drought sensitivity and better adaptation to drought events. Finally, (IIb) growth synchrony was hypothesized to increase towards the cold distribution margin, reflecting the reported increased risk for frost damage and indicating rather limited potential for local adaptation through selection.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

The study was conducted at nine beech-dominated forest sites along a climatic gradient across Europe from the dry to the cold distribution margin of beech (Figure 1). The sites were selected to span across the winter temperature range (February temperature) and precipitation range (average water balance in July) of beech (using data averaged over the period 1960–1990 from the 'ClimateEU' 4.63 software package, available at <http://tinyurl.com/ClimateEU>, based on the methodology described by Wang, Hamann, Spittlehouse, & Carroll, 2016; Figure 1). The elevation of the sites ranged from 44 m a.s.l. in northern Germany to 1,041 m a.s.l. in Spain, whereas soil texture ranged only from poor silty sand in OM (Spain), HH (northern Germany) and VI (Sweden) to sandy silt in NE (Switzerland) and BA (southern Germany) (Table 1; Table S1). The sites were neither very young nor very old (series length [I_{series}] in Table 1; Figure S3). In autumn 2015, at least 19 co-dominant and dominant trees were sampled at eight sites, whereas site NN in southern Germany was sampled in March 2014 (Table 1).

Two increment cores per tree were taken at breast height (1.3 m above ground level). After air drying the cores, they were fixed on wooden mounts and sanded with progressively finer sand paper in order to highlight annual ring boundaries. The cores were scanned at high resolution (Mikrotek ScanMaker 1000XL plus at 1,200 dpi). Ring widths were measured and cross-dated using the software CooRecorder and CDendro (version 8.1, Cybis Elektronik and Data AB 2015). The tree-ring series of the two cores per tree were averaged and all tree-ring series were detrended applying a cubic smoothing spline with a 50% frequency cut-off at 30 years. The detrending process reduced long-term trends such as age, competition and management effects (Cook & Peters, 1981). Afterwards, an autoregressive model was applied to accentuate the high-frequency (year-to-year variability) climate signal. Site chronologies were built by averaging (bi-weight robust mean) over individual tree-ring series. The analyses were done in R 3.4.4 (R Core Team, 2018) using the 'dplR' package (Bunn, 2008). The chronology statistics can be found in Table S2.

2.2 | Climate data

For our study sites, we obtained E-OBS 0.25°× 0.25° gridded climate data including daily precipitation sums as well as daily mean, minimum and maximum temperatures for the common observation period between 1950 and 2015 (Haylock et al., 2008, version 14.0, downloaded from <https://www.ecad.eu/download/ensembles/download.php> on 10/05/2017). E-OBS is a gridded climate data set interpolated from climate station data across Europe (Cornes, van der Schrier, van den Besselaar, & Jones, 2018). In order to exclude potential artefacts that arise using gridded climate data, we referenced the gridded climate data to air temperature data directly measured at all our sampling sites (1 m above ground, November 2015–November 2016, VP-4 Sensor for atmospheric temperature (Decagon Devices, METER Group), EM 50 Data Logger (Decagon Devices, METER Group), Table S3 for detailed description). We used these local field measurements to assess by cross-correlation whether gridded E-OBS climate data or nearby climate station data were more equivalent to the site-specific daily temperature conditions. In most cases, the gridded E-OBS data were equally or better suited to represent local site conditions than nearby climate station data. This assessment also showed that there were no structural differences in the gridded E-OBS data and the field measurements (both were highly correlated; $r > 0.93$ – 0.99 ; Table S3). We also checked the absolute differences in temperature as well as for seasonal trends in the data and concluded that a seasonal trend is not responsible for the high correlation (the visual comparison of the daily absolute minimum temperature can be seen as an example in Figure S1). We used our local temperature measurements to fine-calibrate the gridded E-OBS temperature data to the local field conditions by regression modelling. From these calibrated daily temperature time series, we calculated time series of the absolute minimum temperature and

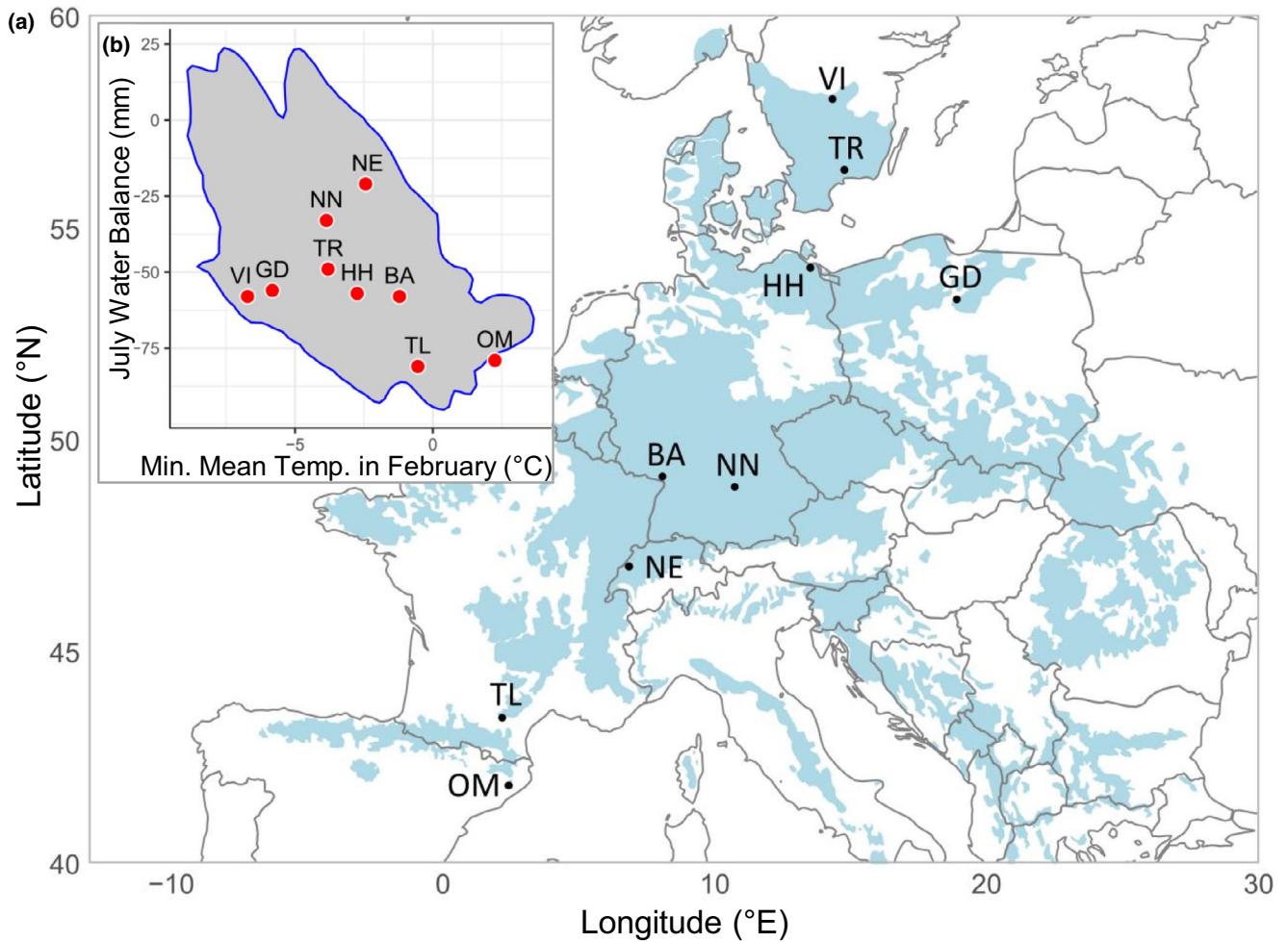


FIGURE 1 (a) Site locations (black dots) within the distribution range of European beech (blue area, EUFORGEN, 2009). (b) Climate envelope of European beech based on 95 percentile of species occurrence data (on EUFORGEN, 2009) and gridded European climate data (climateEU data averaged over the period 1960–1990)

TABLE 1 Site characteristics following the SW–NE study gradient. Geographic position (longitude degree [°E], latitude degree [°N], elevation [Elev.]), number of dated trees (N_{Tree}), tree height (h), diameter at breast height (DBH) and series length (I_{series})

Site ID	Site	°E	°N	Elev. (m a.s.l.)	N_{Tree}	h (m)	DBH (cm)	I_{series}
OM	Obaga Matagalls	2.41	41.81	1,041	20	19.6 ± 1.5	37 ± 4	76 ± 12
TL	Toulouse	2.18	43.41	709	23	26.4 ± 1.8	42 ± 5	108 ± 6
NE	Neuchâtel	6.84	46.98	707	20	30.4 ± 3.7	63 ± 6	99 ± 9
BA	Barbelroth	8.07	49.11	181	20	27.6 ± 2.5	57 ± 20	94 ± 15
NN	Nördlingen	10.74	48.87	565	20	28.3 ± 0.8	39 ± 5	129 ± 6
HH	Hanshagen	13.51	54.05	44	27	31.7 ± 2.3	43 ± 6	76 ± 5
GD	Golub-Dobrzyń	18.90	53.30	113	26	32.3 ± 2.9	56 ± 8	115 ± 13
TR	Tranemåla	14.77	56.36	136	24	26.4 ± 1.5	45 ± 7	141 ± 13
VI	Visingsö	14.33	58.03	135	19	30.6 ± 1.7	47 ± 6	98 ± 11

average temperature of each month during the period 1950–2015. We further subtracted monthly potential evapotranspiration data (estimated from calibrated monthly average temperature using Thornthwaite's equation, Thornthwaite, 1948, R-package 'SPEI',

Beguería & Vicente-Serrano, 2017) from the E-OBS precipitation data to calculate time series of monthly water balance. In addition, we calculated the Standardized Precipitation Evapotranspiration Index (R-package 'SPEI') from these time series of monthly water



balance. Finally, we averaged absolute February minimum temperature, absolute May minimum temperature and water balance in July over our observation period between 1950 and 2015 to characterize our study sites with regard to the average climatic conditions.

2.3 | Climate sensitivity

We assessed the climate–growth relationships for winter cold, spring cold and summer drought over our common observation period from 1950 to 2015 by correlating growth to monthly absolute minimum temperatures during winter (previous December, January or February) and in spring (April or May), and to SPEI in summer (June, July or August) respectively. The climatic parameters were chosen based on the reported sensitivity of beech growth to drought and winter as well as spring frost (Bolte et al., 2007; Jump, Hunt, & Peñuelas, 2006; Scharnweber et al., 2011). For each site, we subsequently selected the month of the strongest response in each factor. This strongest response was correlated against the long-term average climate (period 1950–2015) of each site (average February minimum temperature, average May minimum temperature, average July water balance, respectively) to test for spatial trends in the strength of the relationship between growth and climate across study sites. Additionally, we tested for temporal trends in growth–climate relationships by re-calculating the above climate–growth correlations in a 25-year moving window analysis for each site. All climate–growth correlations were tested for significance in a 1,000-fold bootstrapping procedure (R-package ‘psych’, Revelle, 2018). For these and all of the following statistical analysis we used a significance threshold of $p < 0.05$.

We further assessed spatial trends of site-wide growth reductions, so-called ‘negative pointer years’. We identified negative pointer years with Cropper’s (1979) ‘normalization in a moving window’ method (R-package ‘pointRes’, van der Maaten-Theunissen, van der Maaten, & Bouriaud, 2015) for our observation period from 1950 to 2015. This method z-transforms (setting mean to zero and standard deviation to one) the raw individual tree-ring series. We considered a year to be a negative pointer year if at least 50% of all trees at a given site showed at least weak growth reductions ($z\text{-unit} \leq -1$, Neuwirth, Schweingruber, & Winiger, 2007). Subsequently, we calculated the probability of negative pointer years for each site (number of detected negative pointer years divided by observation period). We regressed this probability against the site-specific average winter cold (minimum February temperature) and average summer drought conditions (water balance in July) respectively. We tested for spatial trends across sites with generalized linear modelling to account for the binomial probability distribution.

In a similar manner to the analysis of the site-wide growth reductions, we assessed spatial trends of site-wide growth synchrony. Therefore, we calculated the inter-series correlation (average pairwise correlation of tree-ring series, \bar{r}) for each site as a measure

of site-specific growth synchrony. We again tested for spatial trends with linear modelling by regressing synchrony against site-specific average winter cold and average summer drought conditions respectively.

3 | RESULTS

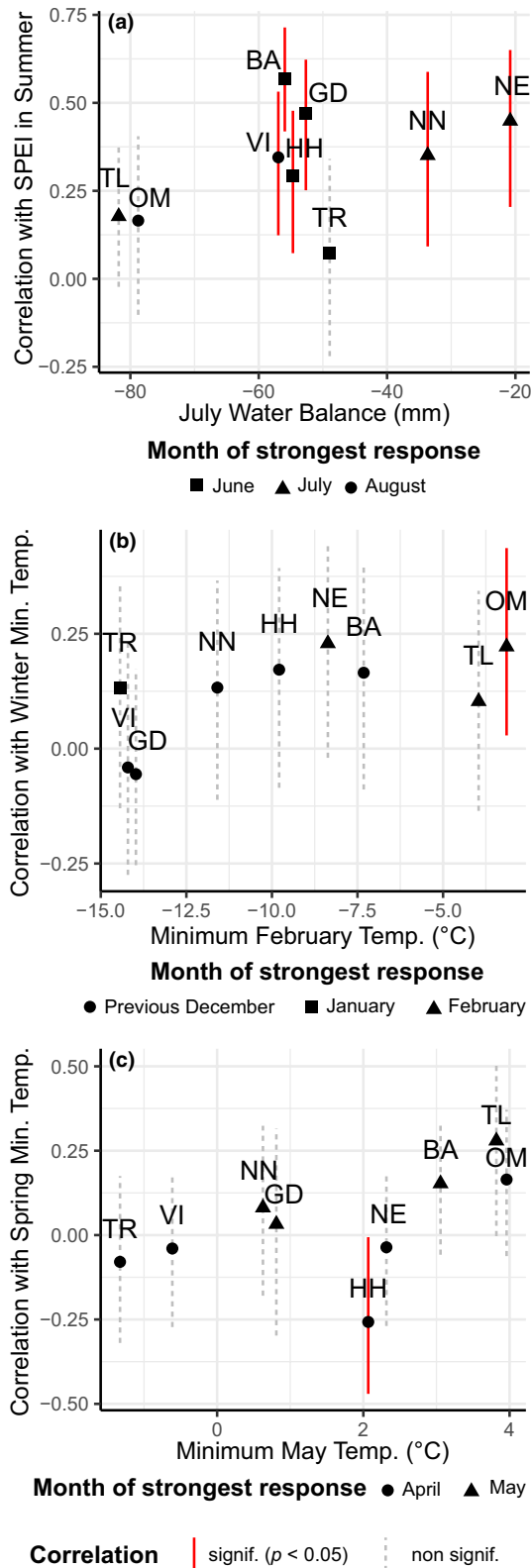
3.1 | Drought and cold sensitivity towards the distribution margins

Drought during summer (SPEI) had a significant negative impact on growth at all sites of the gradient except for site TR in Sweden and the two driest sites TL and OM (Figure 2, for detailed information on the monthly correlations see Figure S2). The most pronounced drought signal (strongest growth response to SPEI in June; significant throughout study period) was found at site BA in southwestern Germany (Figures 2 and 3). Likewise, the drought signal persisted over time at the sites LB, NN and GD. In contrast, a drought signal occurred only occasionally at the driest sites TL (from the 60s to the 90s) and OM (from the mid-50s to the 80s) and was not detected in the most recent years (Figure 3). A drought signal (SPEI) at the site HH in northern Germany in July and August faded out in the late 90s in the moving window analysis (Figure 3), while growth was most strongly responding to SPEI in June when analysing the whole observation period (Figure 2). Growth at site VI in Sweden was mainly influenced by drought (SPEI in July and August) in the first half of our observation period (Figure 3). Mean ring width was lower at the drier sites than at the colder sites (Figure S3).

Winter cold had no impact on tree growth in the centre and at the coldest sites (Figure 2). Only at the warmest site (OM in Spain) did we detect a positive correlation between tree growth and the absolute minimum temperature in February (Figure 2). This signal appeared in the 80s and continues until the present (Figure 3).

Minimum spring temperatures, that is, our proxy for late frost risk, appeared to increase in its importance over time at warmer sites, shown by a significant correlation between tree growth and minimum spring temperature in recent years. It was not being a significant factor at colder sites. From the 1980s until present, years with lower absolute minimum temperatures in April had higher tree growth at the central site HH (Figure 3). In contrast, growth increased with higher absolute minimum temperatures in spring (April and May) in OM since the late 70s and in TL and BA since the late 80s (Figure 3).

The probability of negative pointer years increased significantly from the dry distribution margin to the wettest sites of the gradient and from the warm to the cold distribution margin (Figure 4). In the common observation period from 1950 to 2015, no negative pointer years occurred at the dry distribution margin (OM, TL), whereas the highest probability of negative pointer years was detected in the centre of the distribution range (NN and BA in southern Germany).



3.2 | Growth synchrony from the dry to the cold distribution margin

Growth synchrony increased from the dry distribution margin to the wettest sites of the gradient (Figure 5). Furthermore, growth synchrony decreased from the cold to the warm distribution margin.

FIGURE 2 Growth response to (a) drought (SPEI) in summer (June, July and August in the current year) (b) absolute minimum temperature in winter (December in the previous year, January and February in the current year), and to (c) absolute minimum temperature in spring (April and May in the current year). We selected the month with the strongest correlation and the significance threshold was ≤ 0.05 . The sites on the x-axis are ordered in (a) from sites with lower water balance to sites with higher water balance in July, in (b) with increasing absolute minimum temperature in February (averaged over the period between 1950 and 2015), and in (c) with increasing absolute minimum temperature in May (averaged over the period between 1950 and 2015). The uncertainty intervals (95%) for each site were calculated by a 1,000-fold bootstrapping procedure. The climatic parameters on the x-axis were averaged over the common observation period from 1950 to 2015

Overall, growth synchrony was highest at the wettest sites (NE, NN) and lowest at the driest sites (OM, TL).

4 | DISCUSSION

4.1 | Decreasing drought sensitivity towards the dry distribution margin

As hypothesized, growth responded to drought across the whole distribution range, except for the dry distribution margin. Our observation of decreasing drought sensitivity towards the southern distribution margin in Spain contrasts the often reported growth limitations of beech by drought at the equatorial edge, especially at lower altitudes (Di Filippo et al., 2007; Jump, Hunt, & Peñuelas, 2006; Piovesan et al., 2008; Roibu, Popa, Kirchhefer, & Palaghianu, 2017). However, recent studies have indicated a more complex picture at the equatorial margin (Cavin & Jump, 2016; Hackett-Pain & Friend, 2017). Cavin and Jump (2016) found that beech at the equatorial edge seems on the one hand relatively resistant to drought, but on the other hand shows also a lower recovery after a drought event than the populations in the centre of the distribution range.

We suggest that the weaker climate–growth relationships in our study may result from local adaptation to drought (Cavin & Jump, 2016; Dittmar et al., 2003; Hackett-Pain & Friend, 2017; Thiel et al., 2014). This adaptation might be expressed by conservative growth strategies, which we observed for dry-marginal populations which had the lowest average growth rates (Figure S3). Alternatively, beech might persist in these equatorial populations as climate relicts profiting from local climate conditions (Hampe & Jump, 2011). For example, Barbeto, Camarero, Sangüesa-Barreda, Muffler, and Peñuelas (2019) found that fog had a positive impact on growth of beech in the Montseny Natural Park in Spain, where our most southern site is located.

High growth synchrony within- or across-sites can be used as indicator for the presence of a strong common climatic driver and growth limiting conditions at site or regional level (Andreu et al., 2007; Macías et al., 2006; Shestakova et al., 2016). We found the lowest growth synchrony towards the dry distribution margin. This suggests

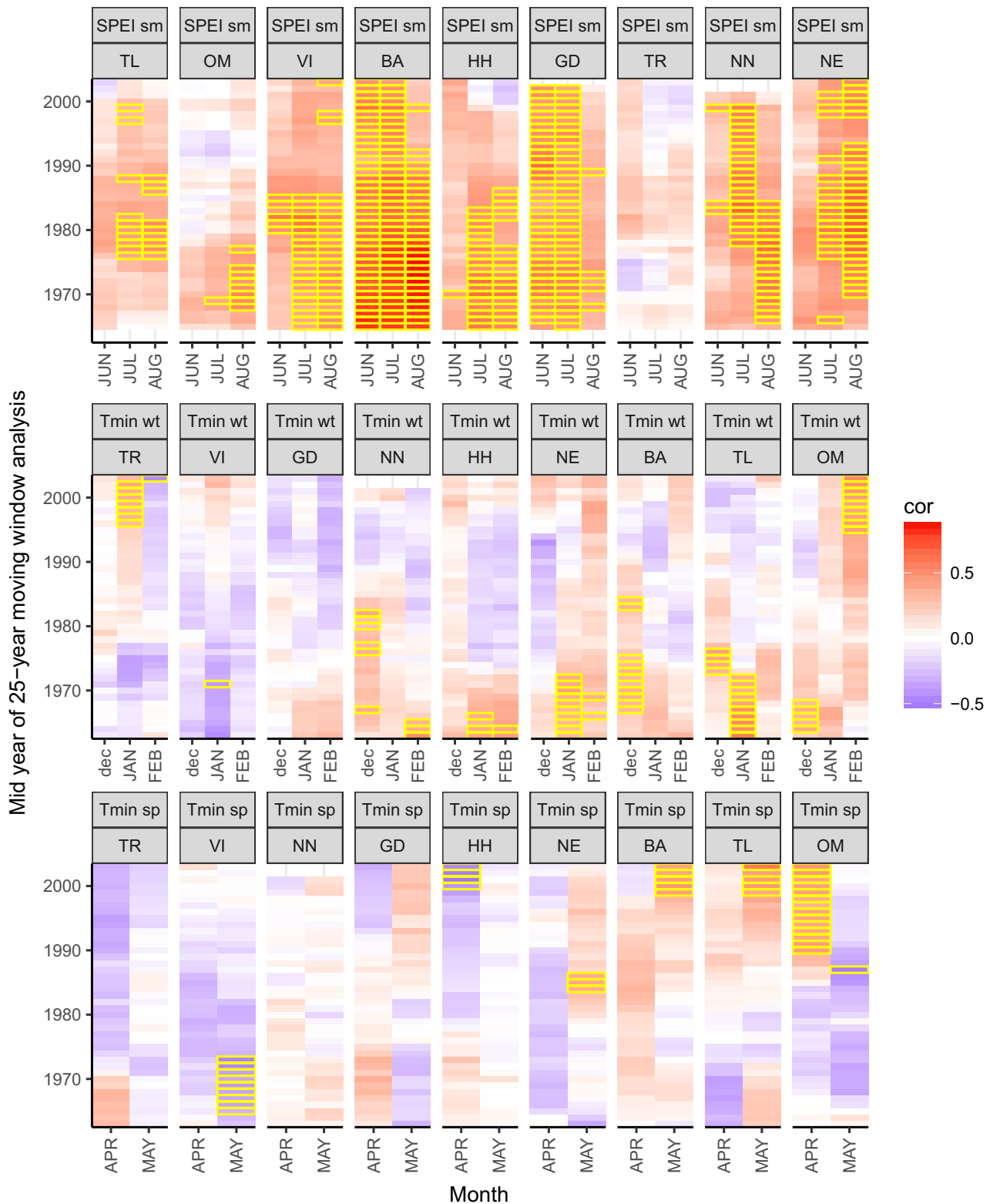


FIGURE 3 Moving window (25 years) analysis of climate–growth relationships. The correlation for site NN stops earlier, as it was sampled in March 2014. Months in lowercase letters refer to the previous year, months in uppercase letters to the current year. Significant correlations are highlighted in yellow. Significance was tested for in a 1,000-fold bootstrapping procedure with a significance threshold of $p < 0.05$. Correlations are clustered according to response category (SPEI sm: SPEI during summer, Tmin wt and Tmin sp: absolute minimum temperature during winter and spring) and site (abbreviations of the sites according to Figure 1). Sites were ordered according to the respective climatic parameter: for SPEI from sites with lower water balance to sites with higher water balance in July, for Tmin wt with increasing absolute minimum temperature in February (averaged over the period 1950–2015), and for Tmin sp with increasing absolute minimum temperature in May (averaged over the period 1950–2015)

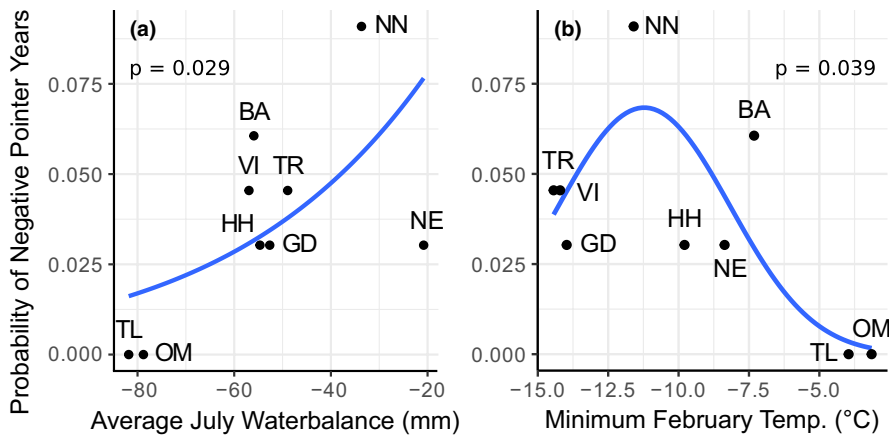


FIGURE 4 Probability of negative pointer years (a) increases towards wetter sites (July water balance), while it is (b) highest for sites with intermediate winter temperatures (absolute minimum temperature in February averaged over the period 1950–2016). Blue lines represent linear fit in (a) and quadratic fit in (b) for generalized linear models with binomial link function

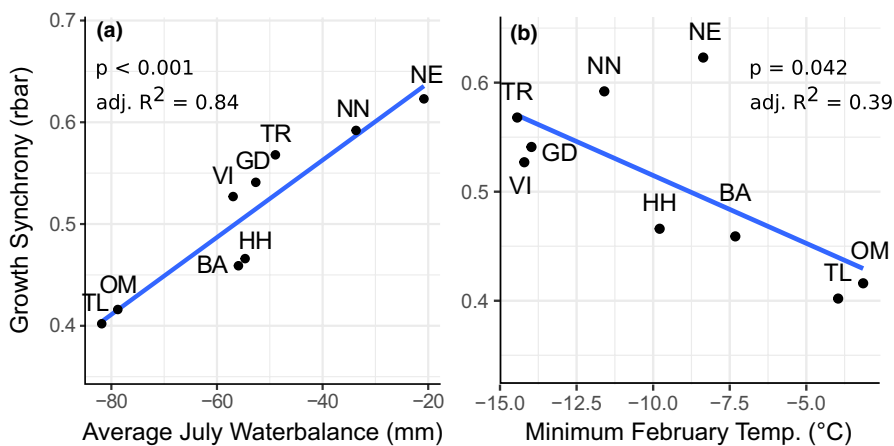


FIGURE 5 Within-site growth synchrony linearly increases (a) towards wetter sites (July water balance) and (b) towards colder sites (absolute minimum temperature in February averaged over the period from 1950 to 2015)

diverse or systematically weaker responses to dry conditions within those dry-marginal populations. Thus, some individuals of these marginal populations might be better adapted to drought and could be favoured by natural selection during rapid climate change (Jump, Hunt, Martínez-Izquierdo, & Peñuelas, 2006). However, microenvironmental heterogeneity and competition for water could be another explanation for the lower growth synchrony towards the warm and dry distribution margin. Indeed, Vilà-Cabrera et al. (2019) argued that the climatic conditions and environmental heterogeneity might be important for explaining population dynamics at the equatorial edge.

Our results suggest that dry-marginal populations are less drought sensitive than central or cold-marginal populations. This is even more remarkable considering the shallow mountain soils at the site in Spain. Therefore, our results call for range-wide reciprocal transplantation experiments in order to explore whether the decreased drought sensitivity at the dry distribution margin is due to local adaptation or due to phenotypic plasticity and small-scale habitat heterogeneity.

The frequency of stand-wide negative pointer years decreased from the wetter sites to the dry distribution margin. Trees of dry-marginal populations with their potentially conservative growth strategy and generally low growth rates might not respond as strongly to extreme climate events as trees of central populations. Moreover, it is striking that the central and cold-marginal populations with their higher average growth rates showed higher growth

synchrony and drought sensitivity. Our European-wide findings are consistent with results from regional precipitation gradients, where stronger drought responses are observed at sites with higher water availability than at the drier sites (Scharnweber et al., 2011). Thus, an increasing likelihood of drought events with climate change (IPCC, 2013), might threaten central populations in particular, not just dry-marginal populations (Cavin & Jump, 2016).

4.2 | Absence of winter cold sensitivity across the distribution range

Winter cold does not appear to be the limiting factor for growth in the centre or at the cold distribution margin, rejecting our hypothesis of increasing cold sensitivity towards the northeastern distribution margin. We only found a winter temperature signal for the warmest and driest site (OM) in Spain and not for cold-marginal populations. The dry-marginal population might be sensitive to even single, mild frost events due to the lack of acclimatization or local adaptation to cold conditions, as the population is genetically separated from the central and cold-marginal populations (Magri et al., 2006). In contrast, this southern population could also profit from an earlier start of cambial reactivation and prolonged xylem growth resulting in enhanced tree growth in warmer years (Begum, Nakaba, Yamagishi,



Oribe, & Funada, 2013; Rossi, Girard, & Morin, 2014). The latter theory is supported by our finding that the February temperature signal appeared in parallel with recent climate warming in the last decades (from the mid-90s on). Furthermore, the population grows on poorly developed, shallow mountain soil. Therefore, growth of beech at this site in particular might be sensitive to the interplay between microbial mineralization rates and root nutrient uptake, which may be driven by soil temperature in late winter and early spring (Sanders-DeMott et al., 2018; Simon, Dannenmann, Pena, Gessler, & Rennenberg, 2017; Yanai, Toyota, & Okazaki, 2004). As these explanations are currently only hypotheses, further physiological analyses and common garden or transplantation experiments are needed.

We did not find an influence of winter cold at any other site, which may be due to beech buds being resistant to extreme frost events (lethal temperature LT50 up to -40°C ; Lenz et al., 2016) that are harsher than any cold events occurring in our study period (up to -31°C in GD in Poland). Quite in contrast to our hypothesis of increasing winter cold sensitivity, drought-mediated growth synchrony increased towards the cold distribution margin. In summary, our findings are in line with Lenz et al. (2016), concluding that winter cold is probably not limiting growth in the climatic gradient studied here. However, it should be noted that an impact of winter cold on beech growth can be observed in cold-wet regions (Weigel et al., 2018), probably due to the above-mentioned reduced root nutrient uptake in colder soils (Augustaitis et al., 2016; Reinmann et al., 2019; Sanders-DeMott et al., 2018; Weigel et al., 2018). This winter cold sensitivity of beech might be masked by a higher importance of drought in our more drought-exposed cold-marginal study sites. Thus, it is crucial to explore the response of northern populations to across-season stressors also on a more regional scale in order to critically assess the consequences of a projected distribution shift of beech beyond its current cold distribution margin (Kramer et al., 2010; Saltr   et al., 2015).

While we did not detect a temporally persistent spring frost sensitivity across the study gradient, tree growth at the site in northern Germany (HH) was even enhanced by cold spring conditions (Figure 2), which probably indicates that low temperatures in April might delay flushing of leaves and thus minimize spring frost risk. A similar, yet not significant trend can also be seen for the sites towards the northern distribution margin (Figure 3). This spring temperature signal appeared in the last decades (Figure 3) showing that the described mechanism is likely becoming more important with climate change. Recent climate warming favours earlier flushing of leaves and thus increases exposition of foliage to spring frost events (Augspurger, 2013; Vitasse et al., 2018) as magnitude and frequency of cold events may persist in future (Kodra et al., 2011; Petoukhov & Semenov, 2010). In accordance with the latter explanation, the trend of a positive correlation between tree growth and the absolute spring minimum temperature became significant towards the south in the last decades (Figure 3). This relationship corresponds to findings of Principe et al. (2017) from Germany, indicating that May is the time when exposition of freshly flushed foliage to frost events may strongly reduce tree growth. Hence, higher absolute minimum temperatures during leaf-out might indicate a lower risk for spring

frost damage. Any increase in the risk of spring frost damage due to climate change is important, as spring frost might be one of the limiting factors of the species' distribution range (Kollas et al., 2014; Lenz et al., 2013; Vitasse, Lenz, & K  rner, 2014). However, the positive response of growth to spring temperature might also be due to a prolonged vegetation period. Our results showed that correlations between spring temperature and growth recently increased in strength, which calls for more detailed analyses of how the interplay of phenological timing and the influence of temperature before, during and after leaf-out changes across Europe. With data on the phenological timing we would be able to differentiate between minimizing the risk of late frost and a prolonged vegetation period when explaining the positive correlation between growth and spring temperature.

5 | CONCLUSION

European beech seems to be adapted to drought at the dry distribution margin with a high adaptive potential indicated by the lowest growth synchrony along the range-wide gradient studied here. Our results of increasing growth synchrony in response to drought for central and northern-marginal populations and interpreting this as lower adaptive potential urgently requires additional research in light of projected climate change. Hence, common garden and transplantation experiments are needed to better understand the potentials and limits of local adaptation and phenotypic plasticity in beech in times of climate change. Surprisingly, winter and spring cold played a minor role in explaining tree growth for central and cold-marginal populations in our study. Still, the importance of spring frost for beech growth appears to increase over time. Considering a projected north-eastward shift of the distribution range, beech is likely facing drought stress in combination with spring frost risk at the cold margin which could lead to a hampered range expansion. On the other hand, a range contraction at the southern margin might be slower than expected due to the drought tolerance of the mature trees. Thus, our tree-ring approach can provide valuable knowledge on environmental stressors and adaptation potentials at range margins which could improve projections of distribution range shifts.

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DATA AVAILABILITY STATEMENT

All chronologies of tree-ring series used for the analyses in this manuscript are uploaded to the DRYAD database (<https://doi.org/10.5061/dryad.3bk3j9k9c>).

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BIOSKETCH

Lena Muffler is interested in global change and the impact of extreme weather events (winter cold, late frost and drought) on forest ecosystems. In her PhD studies she focuses on the in situ responses of European beech (i.e. local adaptation and phenotypic plasticity) to environmental changes by applying a combination of various methods such as ecological experiments, dendroecology and statistical modelling. She and the co-authors collaborate on questions on the response of tree species to climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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